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ASPECTS OF THE BIOLOGY OF THE GIANT FORM OF *STHENOTEUTHIS OUALANIENSIS* (CEPHALOPODA: OMMASTREPHIDAE) FROM THE ARABIAN SEA

R. SNŸDER
British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road, Cambridge CB3 0ET and Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB9 2TN
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ABSTRACT

An investigation was carried out on the recently discovered 'giant' extra large (XL) form of the squid *Sthenoteuthis oualaniensis* from the Arabian Sea. The sample consisted of 2 males, which have not been previously described, and 13 females. Diet composition, parasite loading, sucker ring dentition, bioluminescence and sexual dimorphism were examined and compared to known parameters of the medium (M) form. Reproductive strategy, potential fecundity, egg size distribution in the ovary and oviducts were examined in mature XL females. Evidence of multiple spawning in the giant form was also investigated. Overall body shape, bioluminescent structures and coloration of the giant form were similar to the M form, though the XL form had a smaller fin angle than the M form. The mature female XL form has a dorsal mantle length about twice that of a mature female M form. Adult females of the XL form have a dorsal mantle length about twice that of adult males of the same form. Differences between males and females were found in arm sucker ring dentition and parasite load, suggesting a difference in diet. This could be linked to size differences between the sexes. A strong correlation between ovary mass and mantle length was found ($r^2 = 0.64$). Poor correlation was found between mantle length and oviduct mass ($r^2 = 0.128$) and potential fecundity ($r^2 = 0.07$). Potential fecundity ranged between 2–5 million eggs and the holding capacity of the oviducts was approximately 300,000 eggs. This combined with the presence of spermatangia and the presence of food in the stomach suggest that the XL form is a multiple spawner. *S. oualaniensis* appears to have a plastic phenotype and has adapted to the Arabian Sea conditions by evolving the capacity to grow to a giant size.

INTRODUCTION

The oceanic ommastrephid squid *Sthenoteuthis oualaniensis* (Lesson, 1830) is one of the most abundant squid in the tropical Indo-Pacific. It is a top predator in the tropical oceanic food chain, occupying a similar ecological niche to predatory fish. It occurs from the Red Sea to Australia and from the west coast of Central America to the east coast of Africa, occupying a band about 40° north and south of the equator (Roper *et al.*, 1984). However, it has a patchy distribution, being concentrated in areas of high productivity (Nesis, 1977).

Until recently, two forms of *S. oualaniensis* had been documented. The typical or medium (M) form was first described by Lesson in 1830. Its distribution encompasses most of the known range of the species. It is characterised by the presence of a dorsal photophoric patch and fused mantle locking apparatus (Clarke, 1965). The dorsal mantle length (ML) of adult (sexually mature) males is 120–150 mm and of females 190–250 mm. A second form was documented by Clarke (1965). This is smaller than the M form, with an adult ML in males of 90–100 mm and in females of 90–120 mm. It is termed the early maturing (EM) form and lacks the dorsal photophoric patch. Its distribution appears to be limited to the equatorial region (10–15° N and S) of the Indo-Pacific Ocean, (Nesis, 1977). These two forms are sufficiently different morphologically to constitute separate species (Roeleveld, pers. comm.).

Recently, a third giant form of *S. oualaniensis*, with an adult female ML of 300–500 mm, has been documented (Nesis 1993). This was first discovered in 1986 in the Arabian Sea. This giant or extra large (XL) form has the dorsal photophoric patch and fused mantle locking apparatus and its distribution is apparently limited to the Arabian and Red Sea. Nesis (1993) described only females of this XL form which were associated with the oxygen minimum layer and the lower temperatures at depths of 200–300 m. They largely remain at that depth preying on myctophids, though a small part of the population undertakes vertical migrations to feed at the surface at night (Nesis, 1993). This differs from the EM and M forms, in which the majority of the popu-

lation undertake diurnal vertical migrations, feeding at the surface at night (Nesis, 1977; Roper & Young, 1975; Wormuth, 1976). The ML at maturation of the XL form has not previously been documented. The population structure of *S. oualaniensis* appears complex with sub-populations of EM, M, and XL forms whose geographic ranges partially overlap, so some mixing of populations may occur.

To summarise, *S. oualaniensis* has been divided into three forms, two of which are probably separate species (EM & M forms), each of which occupies a different habitat. The third form (XL), on which this study is based, grows to a much larger size than the M form. In this study, the XL form is compared to the M form in relation to several taxonomic characters and diet. Sexual dimorphism is investigated in the XL form. It has been generally accepted that female ommastrephids are single terminal spawners (Arnold, 1984). However, there is indirect evidence that the M form of *S. oualaniensis* is a multiple spawner (Harman *et al.*, 1989) and this is investigated in the XL form. The term multiple spawner, as defined by Harman *et al.*, (1989), is taken as meaning repeated spawning after the initial release of eggs, interspersed with periods when the oviducts are refilled with new mature eggs from the ovary. This occurs during the spawning phase of the animal's life, which is usually terminal in squid. Potential fecundity estimates and egg size of this low latitude species were analysed and compared with a higher latitude ommastrephid such as Illex.

MATERIAL AND METHODS

Samples were collected from the Arabian Sea during the R. V. Discovery Cruise—ARABESQUE UKJ-GOFS 1994. The squid were caught at three stations: A1: 19° 00′N, 59° 00′E; A2: 17° 07.33′N, 61° 31.07′E; A3: 16° 02.2′N, 62° 00′E (Fig. 1). Squid were attracted to the surface at night by the ship's lights, caught by hand jigging and fixed in 3–4% formal saline.

Measurements were made according to Roper & Voss (1983) and included: mantle length (ML) and width, wet mass, head length and width, mantle thickness, fin length and width, fin angle, arm lengths I–IV, tentacle and club length, hectocotylus length, spermatophore length and width, length of sperm reservoir and nidamental gland length. Body mass was recorded to 1 g. Lengths were recorded to 1 mm. Mass of the ovary, oviducts, oviducal and nidamental glands were recorded to 0.1 g.

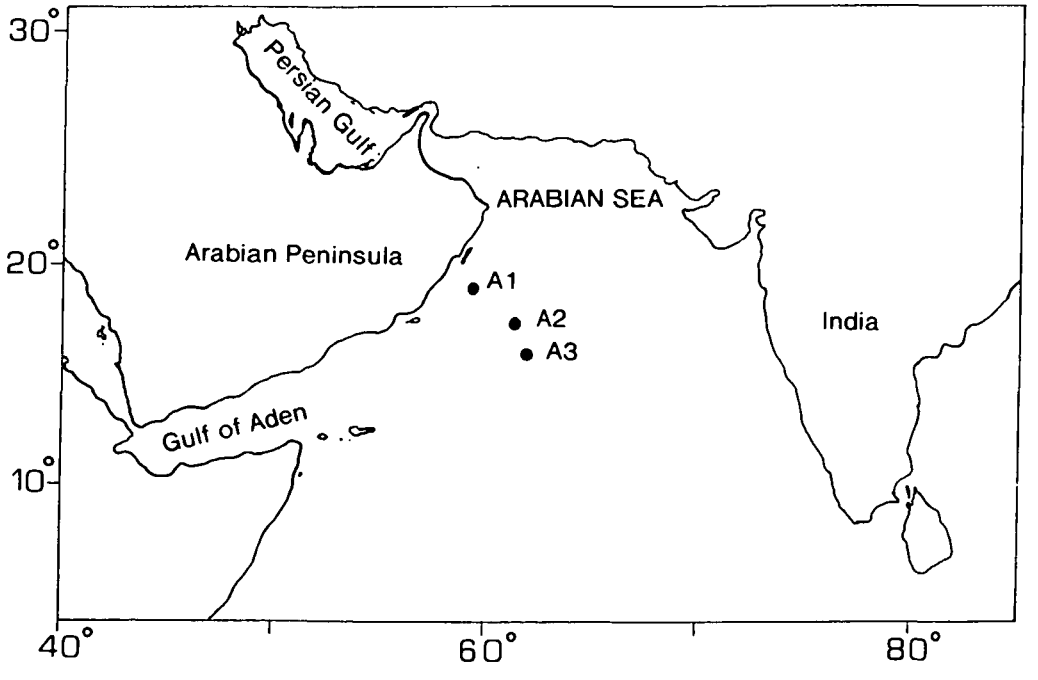

Figure 1. Map of the Arabian Sea showing the positions where the sample of *S. oualaniensis* was collected.

Three types of bioluminescent organs were examined. The dorsal photophoric patch was revealed by peeling back the skin on the antero-dorsal side and cutting into the mantle muscle. Photophores distributed over the whole body were located by removing the skin and dissecting the mantle muscle to a depth of 1 mm. The intestinal photophores which lie on the dorsal side of the intestine were located by teasing the intestine away from the ink sac.

The location and number of internal parasites were recorded and all parasites removed and placed in 70% alcohol for further examination. A sample of parasites was prepared for scanning electron microscopy (SEM). Specimens were fixed in 4% glutaraldehyde solution and then dehydrated in a stepped series of water/acetone solution up to 100% acetone. These were then critical point dried, fixed onto SEM stubs and sputter coated with gold.

The presence and location of spermatangia (the structure containing the sperm reservoir, formed by the eversion of the spermatophore when attached to the female) on the females was recorded. Several spermatangia were removed and examined using SEM.

The largest sucker ring from arms I–IV, carpus, manus and dactylus were removed from a sample of males and females and prepared for SEM.

A subjective estimate of stomach fullness was made on a scale of 1–4 where (1): empty–⅓, (2): ⅓–⅔, (3): ⅔–full, (4): distended stomach (Hatfield, Rodhouse & Porebski, 1990). Stomach contents were classed into three groups: a) fish, b) crustacean, c) squid. Percent composition of each prey group in the stomach was calculated as well as the percent occurrence of each prey group in the whole sample.

Maturity was determined using Lipinski's maturity scales for male and female squid (Juanico, 1983). Only animals at maturity stages 4–5 were examined further. Ovarian samples weighing 25 mg and 50 mg were taken from three areas in the ovary (anterior, centre and posterior) and two areas in the oviduct (anterior and posterior), respectively. Egg sub-samples were separated under a dissecting microscope using fine forceps and counts were made in duplicate. The size (major axis) distribution of the eggs in the ovary and the oviduct was measured using an eyepiece graticule calibrated using a stage micrometer. A detailed examination of egg size distribution from the sample sites in the ovary and oviduct was carried out on a randomly selected animal. The first 200 eggs from each site were measured, the sample pooled, and plotted to give egg major axis frequency distribution in the ovary and oviducts.

RESULTS

Morphology

The sample contained fifteen specimens of the XL form of *Sthenoteuthis oualaniensis*, two males and thirteen females. Mantle lengths of males and females ranged between 174–221 mm ($\bar{x}$ 197.5 mm) and 347–457 mm ($\bar{x}$ 401 mm) respectively. The wet weight range of the males was 145–317 ($\bar{x}$ 231 g), females 1313–3565 g, ($\bar{x}$ 2302 g). Mature females of the XL form were larger in both length and weight compared to the males (See Table 1).

The overall body shape was similar to that described for the M form (Wormuth, 1976). A comparative table of mean body dimensions between the M and XL forms is given in Table 2. The mantle is cylindrical, tapering to a point posterior. In some mature females, the mantle appeared swollen, due to the presence of full oviducts and large nidamental glands. The mantle was thick and muscular. Two females had relatively thinner mantles. The squid all have deep purple coloration on the dorsal side and lighter on the ventral side. The fin width was always greater than fin length, by approximately 20%. The fin angle ranged between 50.5°–59.5° ($\bar{x}$ 55.7°). The funnel was very muscular and both funnel locking cartilages were fused to the mantle. The foveola in the funnel groove was crescent shaped with 5–9 folds. There were 3–6 side pockets present on each side of the funnel groove. The head shape was rectangular and almost square in dorsal view.

The arm formula varied with five animals having I<II≈III<IV, four had I<II≈IV<III, four showed I<III<II≈IV, one had I<II<III<IV and one having I<IV<II<III. Arm I was smallest in all specimens. The sucker count on the arms increased with increasing ML. A comparison between the sucker count of arm pairs I–IV revealed that pairs I and II had a similar mean count (57.3, 56.8), but arm pairs III and IV had a higher mean count (64, 63.4). The largest suckers were found near the base of arm II.

Light organs

The dorsal photophoric patch appeared as a wrinkled oval patch in the mantle muscle and was composed of a single layer of small oval photophoric bodies, each one about 1 mm long. Similar photophoric bodies were found sparsely distributed within the upper muscle layer of the mantle. The density of these photophores was higher in the ventral than the dorsal side. A few of these photophoric bodies were also found in the fins, head and arm I. Two photophores were present on the dorsal surface of the intestine, one proximal to the anus, the other proximal to the stomach. On the ink sac, there were two corresponding iridescent patches. The photophores on the intestine had a diameter of

Table 1. Table of morphometric measurements from the sample of *S. oualaniensis*. All lengths and widths are in mm, weights in grammes..

Sex	f	f	f	f	f	f	f	f	f	f	f	f	f	m	m
Maturity stage	IV–V	IV–V	III	IV–V	III–IV	IV–V	IV–V	II	IV–V	IV–V	II–III	IV–V	IV–V	IV–V	IV–V
Mantle length	457	395	35	422	352	410	435	412	405	401	359	347	392	174	221
Mantle width	125	95	75	115	75	130	110	85	135	95	85	75	8	38	45
Mantle thickness	17	9	11	15	11	11	15	15	16	11	13	8	12	6.5	10
Wet weight	3565	2266	1949	3064	1396	2617	3006	2244	2903	2215	1663	1313	1726	145	317
Head length	91	61	65	81	56	82	92	73	55	65	55	55	53	30	34
Head width	95	65	65	95	65	73	70	65	85	70	72	60	65	32	43
Fin length	250	210	205	215	182	225	215	216	225	185	169	158	185	82	101
Fin width	370	311	306	347	263	319	322	312	305	275	264	224	290	123	176
Fin angle	54°	59.5°	50.5°	55°	55°	57°	54°	57°	55°	58°	55°	55.5°	57°	55°	58°
Arm length I	147	141	143	142	131	145	149	132	150	124	117	111	115	56	64
II	169	155	146	183	152	188	189	165	172	140	134	131	137	68	75
III	176	155	156	158	157	172	187	183	165	139	138	137	137	68	82
IV	185	170	146	186	148	185	197	162	170	152	137	133	146	70	76
Tentacle length	285	292	237	319	235	285	395	395	265	238	233	322	204	141	113
Club length	150	146	141	160	126	160	187	131	145	138	220	141	115	56	55
Hectocotylus length														41	50
Spermatophore length														23	
Spermatophore width														0.8	
Sperm reservoir length														17	
Nidamental gland length	185	172	55	153	85	107	140	61	145	135	45	165	135		

Table 2. Comparison of features between the extra large and medium forms of *S. oualaniensis*. Abbr.: ML; mantle length, LCSD; Largest club sucker diameter, NPI; number of photophores on intestine, DPP; Dorsal photophoric patch present. Morphometric measurements of the medium form taken from Wormuth (1976) and Nesis (1993)*.

Character	Extra large form (x)	Medium form (x)
Mantle length range (♀)	347–457 mm	190–250* mm
Mantle length range (♂)	174–221 mm	120–150* mm
Mantle width/ML	0.242	0.235
Head length/ML	0.169	0.201
Head width/ML	0.186	0.222
Fin length/ML	0.505	0.430
Fin width/ML	0.756	0.790
Fin angle	55.7°	64°
Arm length I/ML	0.335	0.327
Club length/ML	0.370	0.309
LCSD/ML	0.021	0.020
NPI	2	2
DPP	Yes	Yes

3–4 mm, and were different to those embedded in the mantle muscle.

Parasites

Two types of internal parasite were found in the mantle cavity, ovary, stomach lining and internal mantle wall. Most numerous was a larval trypanorhynch cestode, most likely *Nybelinia lingualis* (Hochberg pers. comm.). This larval cestode, 10–23 mm long, 2–3 mm wide, was present in all specimens in the posterior part of the mantle wall and throughout the ovary, but were mostly concentrated near the posterior end of the ovary. Several were also found in the dorsal surface of the connective tissue surrounding the ovary.

The other parasite was an unidentified nematode. These ranged in length from 20–40 mm and 1–2 mm wide. The highest concentration was on the dorsal surface of the spiral caecum where they were tightly coiled in the outer membrane. Others were found in the outer stomach lining and in the anterior part of the ovary which is in close contact to the stomach. Both parasites occurred in all squid and there were fewer nematodes than cestodes. There was a positive correlation between parasite load and increasing ML for females (Fig. 2) ($r^2 = 0.59$ for cestode, $r^2 = 0.67$ for nematode). The parasite load of males was lower than in females.

Sucker ring dentition

A comparison of sucker ring dentition between arm pairs I–IV revealed a similar structure in arms I–IV, but there were some differences in one sample of arm IV (Fig. 3). There were 6–8 large teeth in the distal region of the ring. The size of these teeth was uniform, but varied in relation to sucker size. However, these are distinct differences in the dentition pattern between males and females. Female arm sucker ring dentition is characterised by having a prominent larger central tooth surrounded by several large teeth in the distal portion of the ring. The proximal region of the sucker ring has a number of smaller teeth (Fig. 3 'f'). One female lacked these smaller teeth on arm IV. Male sucker ring dentition differs in two main respects. They lack the larger central tooth seen in females, and lack any smaller teeth in the proximal region of the sucker ring (Fig. 3 'm'). Examination of the dentition pattern from sucker rings from the tentacular club regions (carpus, manus and dactylus) revealed no structural differences between males and females.

Feeding

Initial examination of the stomach revealed all but one of the squid (ML 221 mm) had recently fed. Over half the squid had full stomachs (⅔–full). Of the mature females, two thirds had a full stomach and one third had stomachs which were ⅓–⅔ full. The immature females also had food in their stomachs. One male had some food in the stomach (empty–⅓ full), the other had an empty stomach.

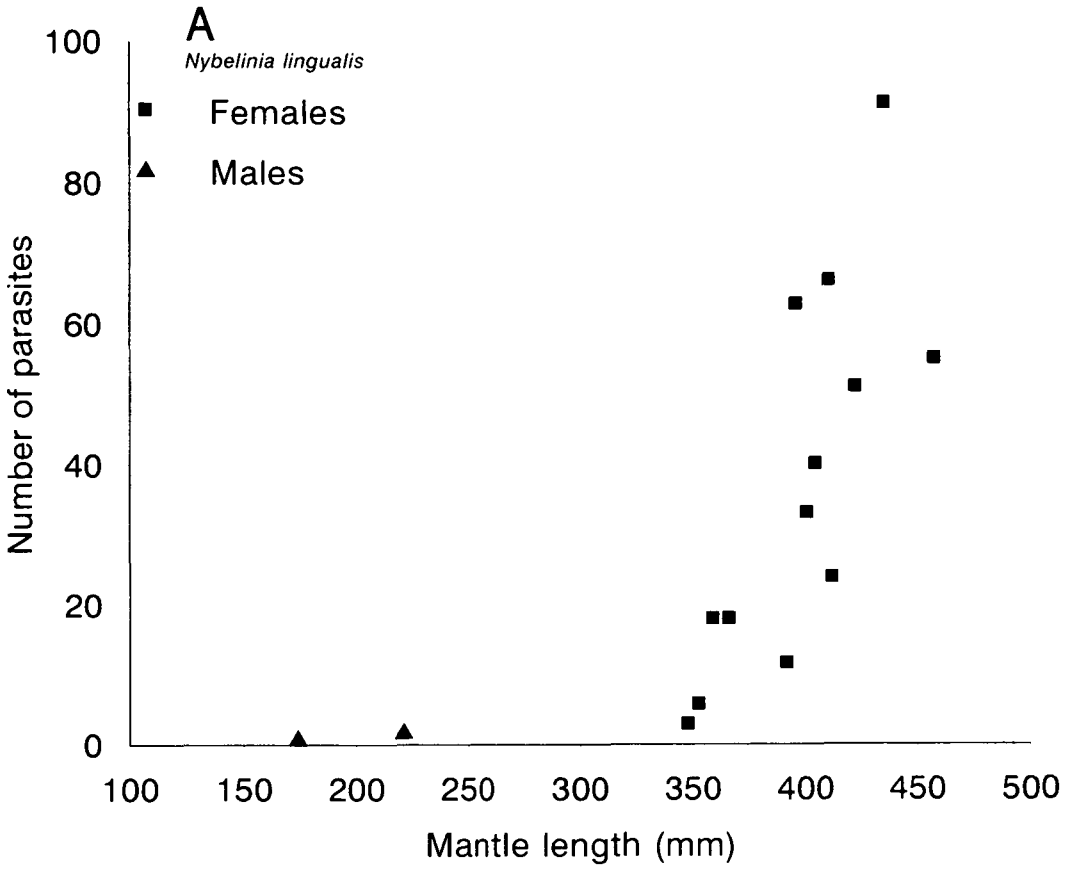

Figure 2. Relationship between parasite loading of *S. oualaniensis* by cestodes **(A)** and nematodes **(B)** and mantle length.

The diet comprised of three components: fish, crustaceans and squid. Fish were identified by the presence of scales, vertebrae and lenses. These were mostly myctophids (White, pers comm). Remains of larger fish were also found, possibly of epipelagic clupeids or scombrids. The crustacean component was composed of pieces of carapace and legs of mesopelagic decapods. The squid component of the stomach contents consisted of beaks, sucker rings and pieces of muscle and gladius. They were all from ommastrephid squid (Rodhouse pers comm), with sucker ring dentition similar to *S. oualaniensis*.

The percentage contribution of each component to the diet of each squid is given in Table 3. Fish and crustaceans comprised the largest part of the diet and occurred in all the stomachs which contained food. Squid were common, but contributed only a small percentage of total food present in most animals. Squid occurred in 80% of all the stomachs containing food. The XL form appears to feed primarily on myctophids and crustaceans.

Sexual maturity and fecundity

Mantle length at maturity in females varied considerably in the sample. The minimum ML at maturity (stage IV–V) was 347 mm, although three larger animals (359, 365, 412 mm ML) were immature (stage III). The estimated potential fecundity of *S. oualaniensis* is shown in Table 4. The potential fecundity range (2–5 million eggs) calculated for the XL form fell within the range calculated for the '*Sthenoteuthis* type' squid given by Nigmatullin & Laptikhovsky (1994) of 0.1–22 million eggs. Potential fecundity plotted against ML (Fig. 4) revealed no statistically significant correlation

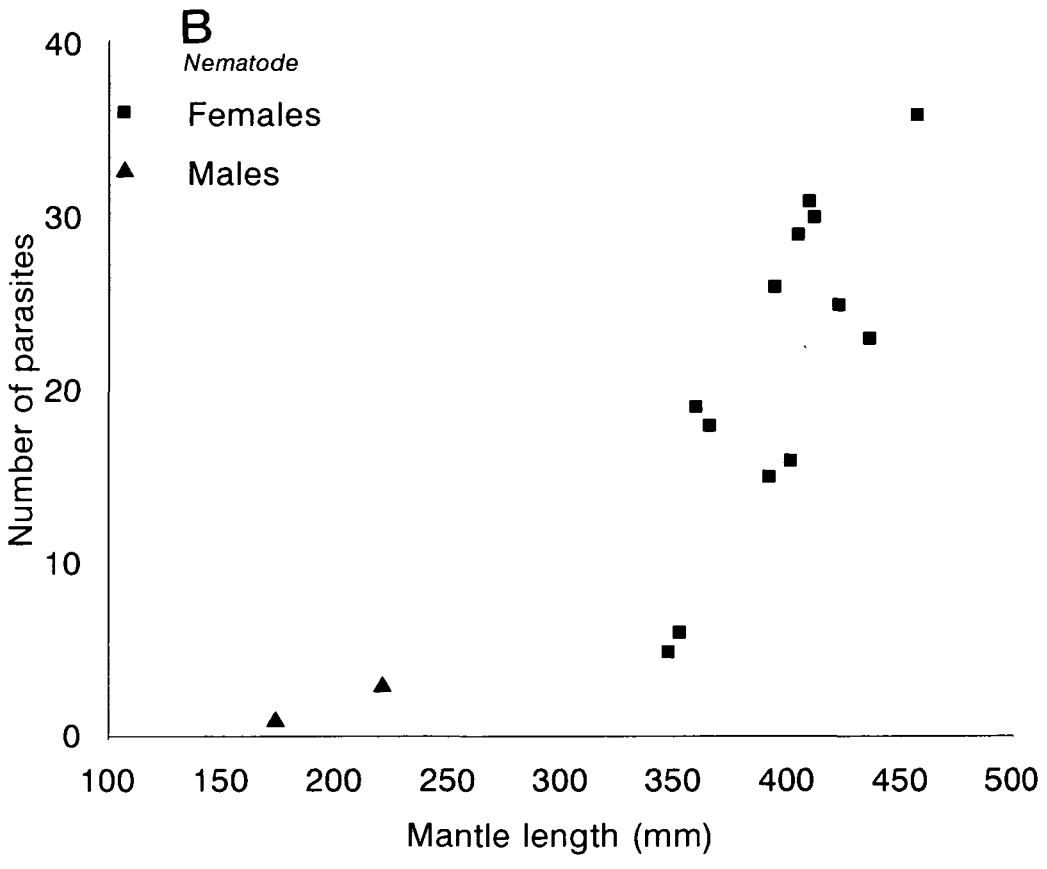

Table 3. Table of percentage composition of the stomach contents of *S. oualaniensis* including mantle length, body weight, maturity stage (MS) and stomach fullness.

Mantle Length (mm)	Body Mass (g)	MS	Stomach Fullness	% Fish	% Crustacean	% Squid
174	145	IV	3	70	25	5
347	1313	IV	3	60	30	10
352	1396	III	3	2	50	48
359	1663	III	3	50	45	5
365	1949	III	3	35	60	5
392	1726	IV	2	50	50	0
395	2266	IV	3	25	70	5
401	2216	IV	3	10	60	30
405	2903	IV	3	45	45	10
410	2617	IV	3	40	55	5
412	2244	III	1	80	5	15
422	3064	IV	3	10	85	5
435	3006	IV	2	95	5	0
457	3565	IV	1	60	20	20

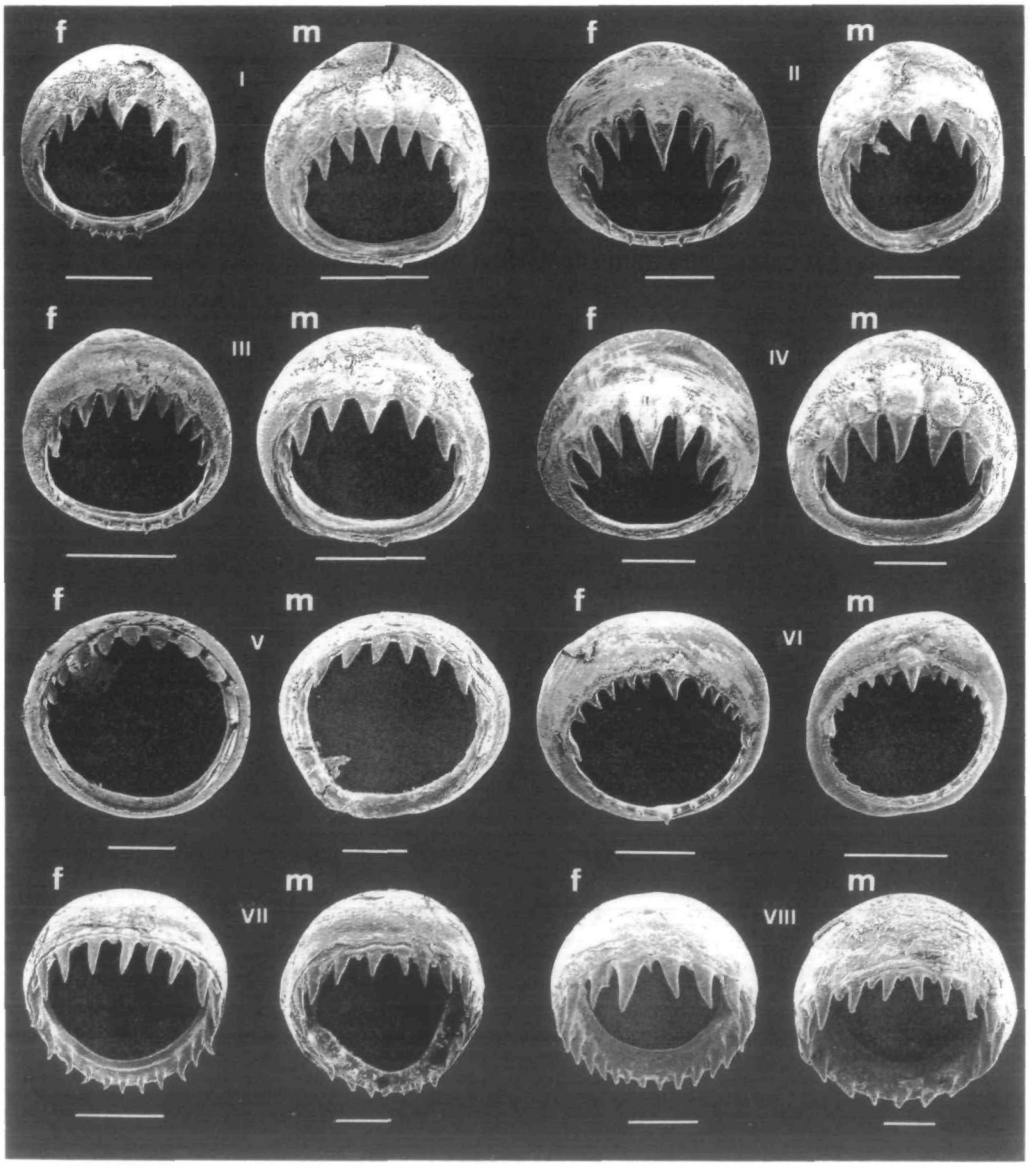

Figure 3. Micrographs of inner sucker rings from *S. oualaniensis* taken from arms I–IV, carpus, manus and dactylus of the club, showing the characteristic dentition patterns of both females **(f)** and males **(m)**. I–IV are the largest suckers from arms I–IV; V, VI, VII and VIII are from the carpus, manus (median and lateral suckers) and dactylus respectively. Scale bars for If, IIf, IIIf, IVf, VIf = 2 mm; Im, IIm, IIIm, VIm, VIIf = 1 mm; VIm, Vf, VIIIf = 500 μm; Vm, VIIm, VIIIm = 200 μm.

between the two (r^2 = 0.07). Fig. 5 shows the relationship between ovary weight and ML in which revealed a strong correlation (r^2 = 0.64). There was no statistically significant correlation between oviduct weight and ML (r^2 = 0.128) (Fig. 6).

Frequency distribution of egg major axis in the ovary and oviducts are shown in Fig. 7. Size of eggs in the ovary range from 0.001–0.900 mm, with the majority between 0.08–0.30 mm (major axis). This includes a large proportion of maturing and pre-viteleogenic eggs. The size

Table 4. Table of potential fecundity estimates of mature *S. oualaniensis* with corresponding ovary and oviduct weights and mantle lengths.

Mantle length (mm)	Ovary weight (g)	Oviduct weight (g)	Potential fecundity
347	69.1	80.7	2,020,589
392	45.8	55.7	2,835,936
395	85.2	34	2,940,862
401	75.6	73.5	4,792,872
405	85.7	58.9	3,536,057
410	111.7	23.8	3,305,463
422	98	25.1	4,604,336
435	139.8	54.4	3,368,388
457	145.2	59.1	2,660,017

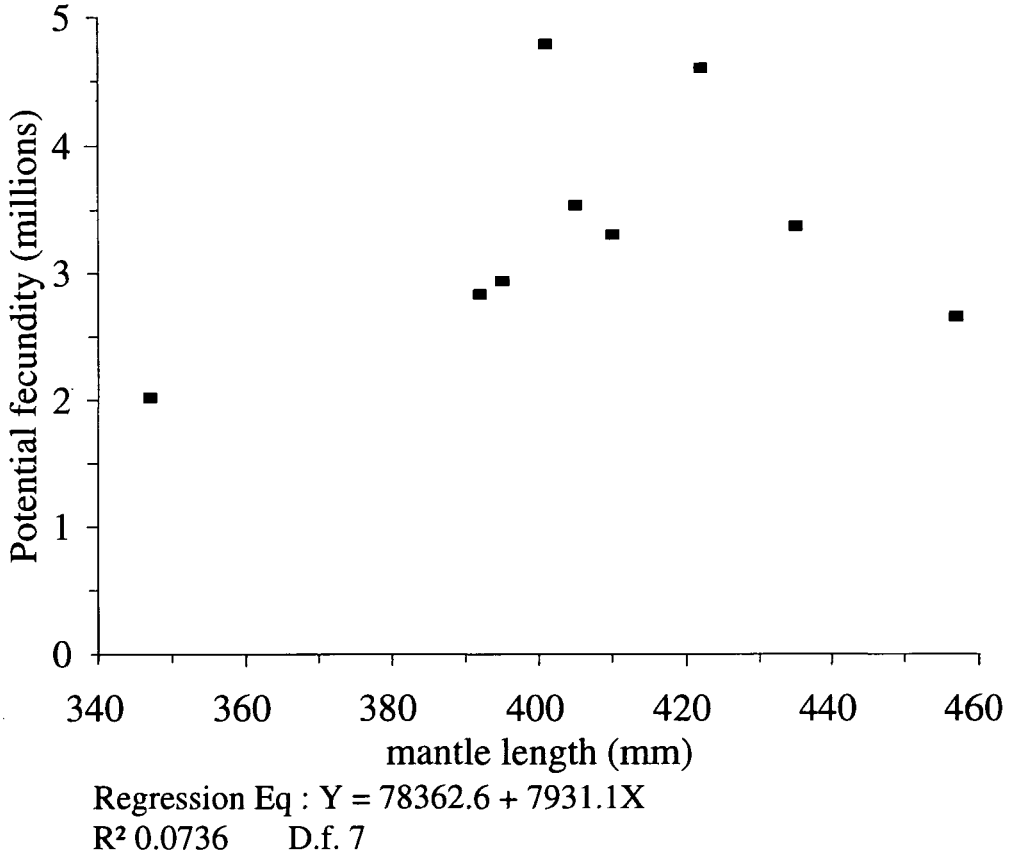

Figure 4. Relation between potential fecundity and mantle length of mature *S. oualaniensis.*

range in the oviducts is narrower, between 0.56–0.90 mm, with only mature ova present.

Empty spermatangia were found on and around the buccal membrane of all the mature females in this study. The spermatangia appeared as small finger like projections 3–4 mm long, 0.5 mm wide at base, 70 μm wide at tip (Fig. 8). They were fixed onto the skin around the buccal membrane of the females. One immature female (ML 412 mm, maturity stage II) also had empty spermatangia present.

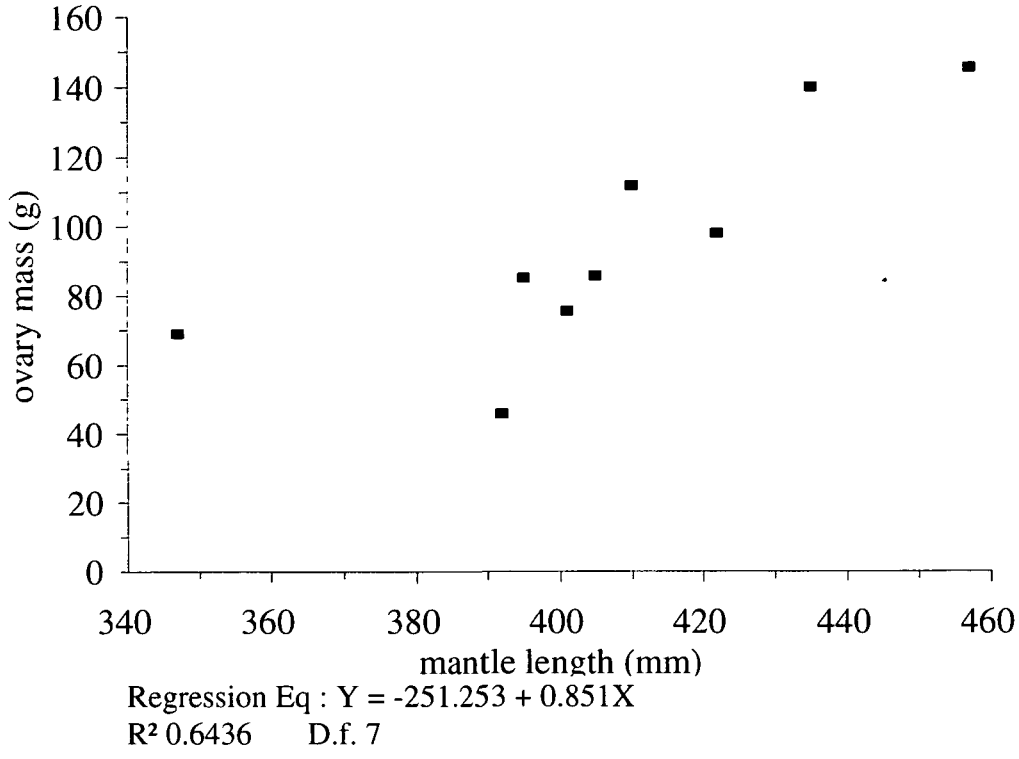

Figure 5. Relation between ovary mass and mantle length of mature adults.

DISCUSSION

Morphologically, the XL form is similar to the M form (Wormuth, 1976; Roper *et al.*, 1984). The general body shapes are similar. The main difference between these two forms is size. The adult XL form has a ML twice that of the M form. Location and presence of photophores are the same in the two forms. Relationships between mantle length and other body dimensions were similar between the two forms. The mean fin angle of the XL form is lower than that of the M form (Wormuth, 1976). The results suggest that *S. oualaniensis* is polymorphic, where the high productivity available in the Arabian Sea has allowed a large increase in size of the phenotype, resulting in the extra large form.

There were several kinds of sexual dimorphism present between males and females of the XL form. The most apparent was the size difference. In this study, males were on average about half the length of females and one tenth their weight. This dimorphism in size is common to all three forms of *S. oualaniensis*, and is a feature common to other ommastrephids (Arkhipkin & Mikheev, 1992).

A second sexual dimorphism was found in the sucker ring dentition of the arms. Females had a larger central tooth in the distal region of the ring and smaller teeth in the proximal region, both of which the males lacked. One function of the teeth is to grip the prey and a difference in dentition may reflect differences in diet between the smaller males and larger females. Suckers and teeth may also be used in interactions between squid such as courtship and the differences in dentition may also reflect this.

There was also a large difference in the parasite loads between the males and females. Females have a higher parasite load than males. This difference in parasite load may not be related to differences in age as males and females were found together leading to the assumption that in this semelparous species they were all from the same cohort. As the main route of infection is via ingestion of infected

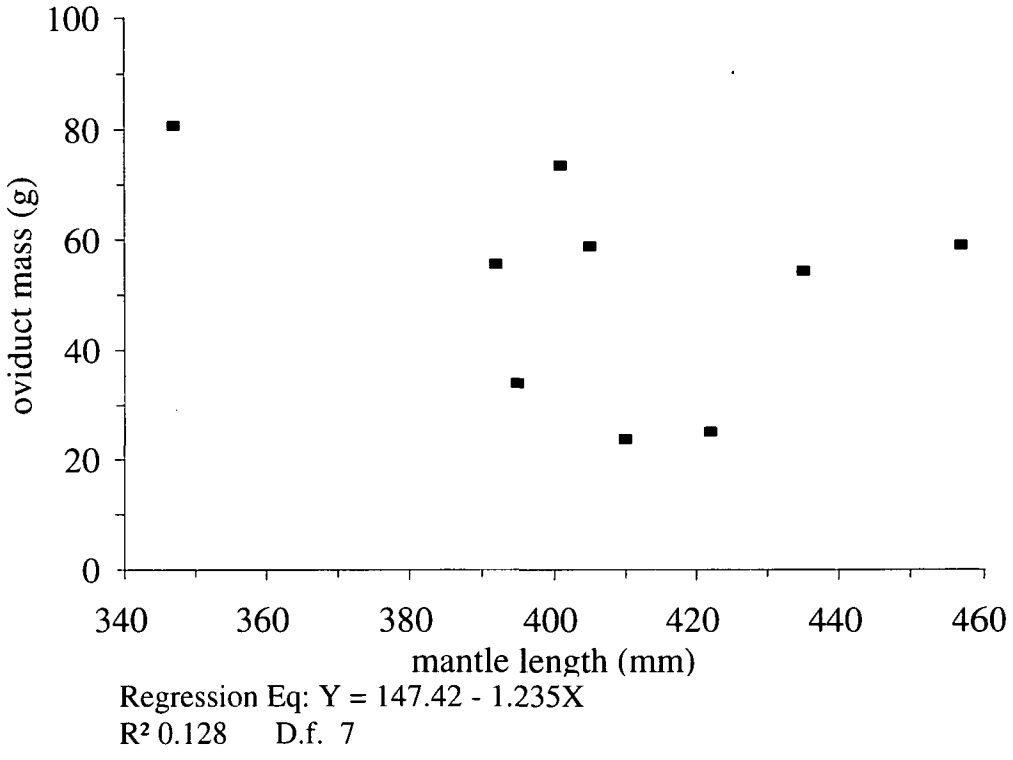

Figure 6. Relationship between oviduct mass and mantle length of mature adults.

prey (Naidenova *et al.*, 1985), a difference of parasite load between males and females may reflect a difference in the feeding spectrum between the two sexes. Prey selection is dependant on predator size and the differences in diet between males and females reflects the size differences. This together with the difference in size and dimorphism in sucker ring dentition, all suggest that there is a difference between the feeding spectrum of males and females of the XL form. There were insufficient data from stomach contents of males and females to confirm this.

The diet of the XL form is dominated by myctophids and large mesopelagic decapods. Squid was also an important component. This differs from the M form where myctophids compose the main part of the diet and crustaceans contribute only a small portion to the adult diet (Schetinnikov, 1992). Squid has a greater importance in the diet of the XL form than the M form. This could reflect differences in abundances of prey species in the Arabian Sea compared to the Indo-Pacific, or differences in the food spectrum available to the XL form.

Data from this sample appear to support the multiple spawning hypothesis (Harman *et al.*, 1989) for the XL form. Evidence for multiple spawning comes from several areas. One is the large size range at maturity of the XL form. This taken in conjunction with the fact that most mature animals had recently fed, suggests that either size at maturity is naturally highly variable or that these animals continue to grow after reaching sexual maturity. A single terminal spawning ommastrephid squid will cease feeding and utilise energy reserves to mature the eggs, resulting in a wasted appearance of the animal at spawning (Laptikhovsky & Nigmatullin, 1993). No animals in this sample appeared wasted, but all mature animals had recently fed and had large amount of eggs in the oviducts.

Other evidence comes from the lack of a strong correlation between ML and oviduct mass in the sample of mature females, an indirect measure of oviduct fullness. However,

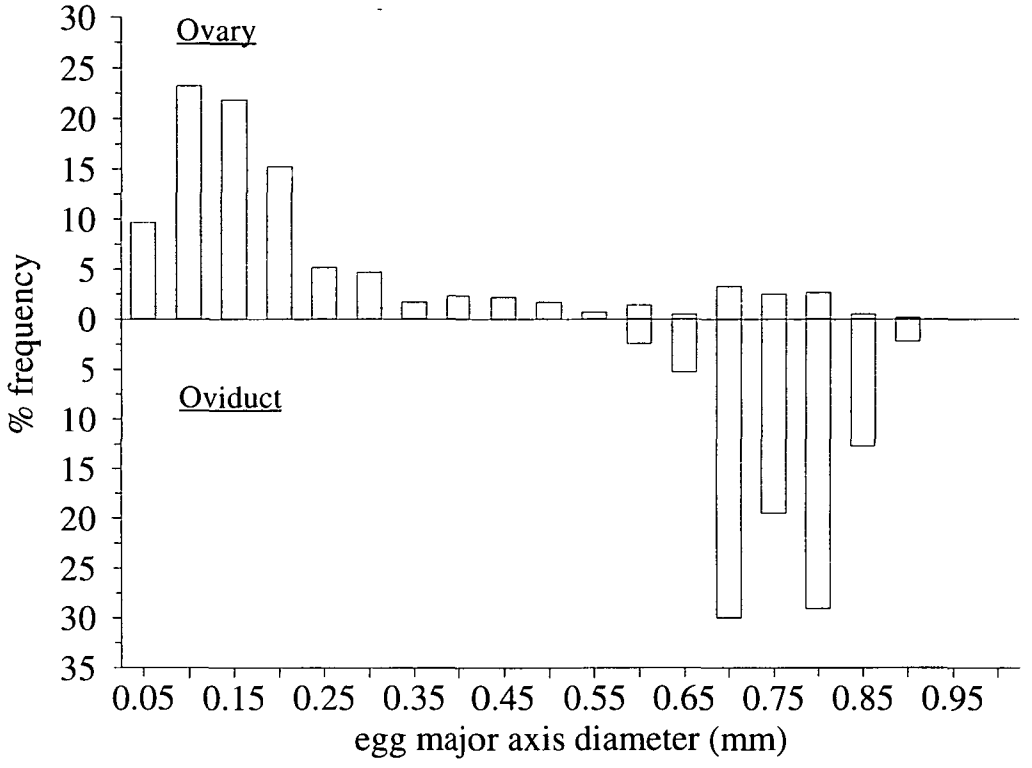

Figure 7. Egg major axis frequency distribuion from samples taken from the ovary and oviducts of *S. oualaniensis.*

there is good correlation between ovary weight and ML. In a mature single terminal spawner, a strong positive correlation would be expected between ML and oviduct fullness, as well as a negative correlation between ML and ovary mass. The findings reveal an almost opposite picture with a positive correlation between ovary mass and ML and poor correlation between oviduct mass and ML. This suggest that eggs are spawned periodically as the animal grows, and the oviducts were in the process of refilling, resulting in a variable oviduct fullness in relation to ML. Ovary mass generally increased with ML, though the largest two animals had a lower potential fecundity than expected, suggesting that they may have previously partially spawned.

One of the main points suggesting that the XL form of *S. oualaniensis* is a multiple spawner is in the potential fecundity estimates. In this study it has been calculated that the XL form has a potential fecundity in the range of 2–5 million eggs. The maximum number of ripe ova stored in the oviducts was approximately 300,000 eggs. It would be physically impossible for the animal to store several million eggs in its oviducts. This suggests that either a large part of the ovary is wasted (if it only spawned once) or that it releases eggs in batches, interspaced with periods of refilling the oviducts. It would seem that the latter scenario is more plausible. *Illex argentinus* probably spawns around 70% of its potential fecundity (Laptikhovsky & Nigmatullin, 1993). It has been suggested that it achieves this by a series of active spawning periods, interspersed with periods in which eggs migrate from the ovary to refill the oviducts during the spawning phase of its life (Laptikhovsky & Nigmatullin, 1993). It appears that the XL form of *S. oualaniensis* has a similar strategy. The presence of empty spermatangia on all mature females reveals that these animals had previously mated and possibly spawned and were presently refilling the oviducts. However, the possibility that spermatophores may have been broken off during

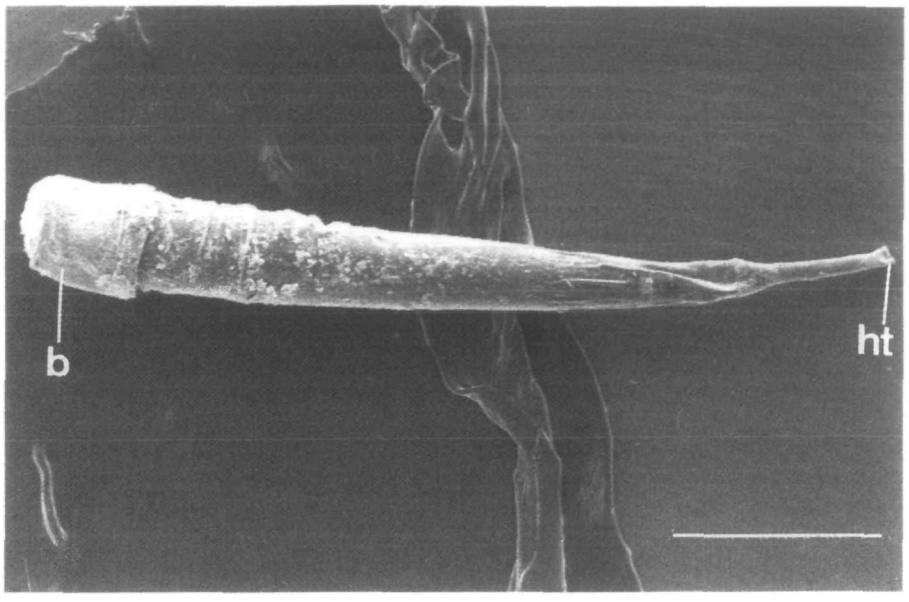

Figure 8. Micrograph of an empty spermatangium from the buccal membrane of *S. oualanienis* showing the general external structure. Scale bar = 1 mm. Abbreviations: b, base (attachment area), ht. Hollow tip.

capture giving a false impression of a previous spawning event cannot be excluded.

The potential fecundity of the XL form in this study was high (2–5 million) and the mature eggs were small (0.6–0.9 mm). This is in contrast to higher latitude oceanic squid such as *Illex argentinus* which produce fewer, larger eggs (Rodhouse & Hatfield, 1990). The potential fecundity of *I. argentinus* ranges between 100,000 to 250,000 eggs, with egg size between 1.3–1.7 mm. By extrapolation, the XL form of *S. oualaniensis* of equivalent size would have a potential fecundity of approximately 1.8 to 2.3 million eggs. Clearly, the smaller egg size and larger body size of the XL form of *S. oualaniensis* combined produce a large increase in potential fecundity.

The presence of three different forms of *S. oualaniensis* in the Indo-Pacific, an early maturing, medium and extra large form, suggests that the phenotype is plastic, allowing the species to best utilise available resources and oceanographic conditions. The XL form lives in an area of the Arabian Sea where a stable oxygen minimum layer exists (Nesis, 1993). This feature is associated with high productivity. Increased size has several advantages including increased potential fecundity and a larger size range of prey species (Rodhouse & Nigmatullin, 1966). Gigantism is generally only possible in stable environments with high productivity where the risk of predation is low (Law, 1979). These all occur in the oxygen minimum layers in certain areas of the Arabian Sea, where phenotype plasticity has given the XL form of *S. oualaniensis* the potential to grow very large indeed (6–8 kg body weight) (Zeuv *et al.*, 1993).

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REFERENCES

ARNOLD, J.M. 1984. Cephalopods. In: The Mollusca. Volume 7: Reproduction. (Tompa, A.S., Verdonk, N.H., & den Biggelar, J. eds), 419-454. Academic Press, Orlando.

ARKHIPKIN, A. & MIKHEEV, A. 1992. Age and growth of the squid *Sthenoteuthis pteropus* (Oegopsida: Ommastrephidae) from the Central-East Atlantic. *Journal of Experimental Marine Biology and Ecology*, **163**: 261-276.

CLARKE, M.R. 1965. Large light organs on the dorsal surfaces of the squids *Ommastrephes pteropus, Symplectoteuthis oualaniensis* and *Dosidicus gigas*. *Proceedings of the Malacological Society London*, **36**: 319-321.

HARMAN, R.F., YOUNG, R.E., REID, S.B., MANGOLD, K.M., SUZUKI, T. & HIXON, R.F. 1989. Evidence for multiple spawning in the tropical oceanic squid *Stenoteuthis oualaniensis* (Teuthoidea: Ommastrephidae). *Marine Biology*, **101**: 513-519.

HATFIELD, E.M.C., RODHOUSE, P.G. & POREBSKI, J. 1990. Demography and distribution of the Patagonian squid (*Loligo gahi* d'Orbigny) during the austral winter. *Journal du Conseil.*, **46**: 306-312.

JUANICO, M. 1983. Squid maturity scales for population analysis. In: Advances in assessment of world cephalopod resources. (Caddy, J.F. ed.), *FAO Fisheries Technical Paper*, **231**: 341-378.

LAPTIKHOVSKY, V.V. & NIGMATULLIN, CH.M. 1993. Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES Journal of Marine Science*, **50**: 393-403.

LAW, R. 1979. Ecological determinants in the evolution of life histories. In: *Population dynamics*. (Anderson, R.M., Turner, B.D. & Taylor, L.R. eds.), 81-104. Blackwell Scientific Publications, London.

NAIDENOVA, N.N., NIGMATULLIN, C.M. & GAEVSKAYA, A.V. 1985. The helminth fauna and host-parasite relations of squids *Sthenoteuthis oualaniensis* (Lesson) (Cephalopoda, Ommastrephidae) in the Indian ocean and the Red sea. In: *Parasitology and pathology of marine organisms of the world ocean*. (Hargis, W.J. (Jr) ed.), *National Oceanic an Atmospheric Administration, Technical report*, 25: *NMFS*: 113-116.

NESIS, K.N. 1977. Population structure in the squid *Sthenoteuthis oualaniensis* (Lesson 1830) (Ommastrephidae) in the western tropical Pacific. *Trudy Inst. Okeanol. P.P. Shirshov*, **107**: 15-28. (In Russian, English summary).

NESIS, K.N. 1987. *Cephalopods of the world*. T.F.H. Publications, Neptune City.

NESIS, K.N. 1993. Population structure of oceanic Ommastrephids, with particular reference to *Sthenoteuthis oualaniensis*: a review. In: *Recent advances in fisheries biology*. (Okutani, K., O'Dor R.K. & Kubodera, T. eds), 293-312. Tokai University Press, Tokyo.

NIGMATULLIN, CH. M. & LAPTIKHOVSKY, V.V. 1994. Reproductive strategies in the squids of the family Ommastrephidae (preliminary report). *Ruthenica*, **4**: 79-82.

RODHOUSE, P.G. & HATFIELD, E.M.C. 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). *Philosophical Transactions of the Royal Society of London*, **B329**: 229-241.

RODHOUSE, P.G. & NIGMATULLIN CH. M. 1996. Role as consumers. *Philosophical Transactions of the Royal Society of London*, **B351**: 1003-1022.

ROPER, C.F.E., SWEENEY, M.J. & NAUEN, C.E. 1984. FAO Species Catalogue, Vol. 3, Cephalopods of the world, An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis*, **125, 3**: 157-181.

ROPER, C.F.E. & VOSS, G.L. 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum Victoria*, **44**: 49-63.

ROPER, C.F.E. & YOUNG, R.E. 1975. Vertical distributions of pelagic cephalopods. *Smithsonian Contributions to Zoology*, **209**: 1-48.

SHCHETINNIKOV, A.S. 1992. Feeding spectrum of squid *Sthenoteuthis oualaniensis* (Oegopsida) in the eastern Pacific. *Journal of the Marine Biological Association of the U.K.*, **72**: 849-860.

WORMUTH, J.H. 1976. The biogeography and numerical taxonomy of the Oegopsid squid family Ommastrephidae in the Pacific ocean. *Bulletin of the Scripps Institution of Oceanography*, **23**: 1-90.

ZUEV, G.V., NIKOLSKY, V.N. & CHESALIN, M.V. 1993. The biology and resources of the purpleback flying squid (*Sthenoteuthis oualaniensis*) in the Arabian Sea. In: *Biogeochemical processes in the Arabian sea*; Arabian Sea workshop, Sevastopol, Crimeae, Ukraine, 167-172.